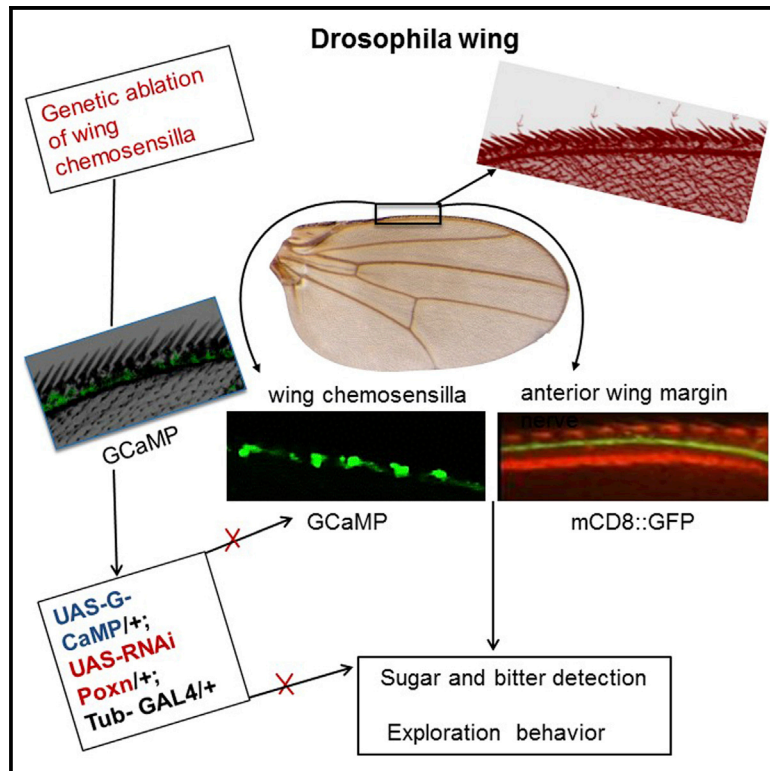


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Functional Gustatory Role of Chemoreceptors in *Drosophila* Wings

Graphical Abstract



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In Brief

The function of *Drosophila* wing chemosensilla is poorly understood. GFP gene reporter assays and electrophysiology are hampered by the nano-architecture of bristles and dense chitin. Raad et al. report that the wing taste organ responds to bitter and sugar stimuli and is critical for exploration of ecological niches.

Highlights

- Expressed GRs in *Drosophila* wing respond to sweet and bitter stimuli
- Genetic ablation of *Drosophila* wing chemosensilla abolishes taste signaling
- *Drosophila* wing chemosensilla constitute a functional taste organ
- *Drosophila* wing taste organ contributes to exploration of ecological niches



Functional Gustatory Role of Chemoreceptors in *Drosophila* Wings

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SUMMARY

Neuroanatomical evidence argues for the presence of taste sensilla in *Drosophila* wings; however, the taste physiology of insect wings remains hypothetical, and a comprehensive link to mechanical functions, such as flight, wing flapping, and grooming, is lacking. Our data show that the sensilla of the *Drosophila* anterior wing margin respond to both sweet and bitter molecules through an increase in cytosolic Ca^{2+} levels. Conversely, genetically modified flies presenting a wing-specific reduction in chemosensory cells show severe defects in both wing taste signaling and the exploratory guidance associated with chemodetection. In *Drosophila*, the chemodetection machinery includes mechanical grooming, which facilitates the contact between tastants and wing chemoreceptors, and the vibrations of flapping wings that nebulize volatile molecules as carboxylic acids. Together, these data demonstrate that the *Drosophila* wing chemosensory sensilla are a functional taste organ and that they may have a role in the exploration of ecological niches.

INTRODUCTION

In *Drosophila melanogaster*, the anterior wing margin harbors two types of sensory bristles arranged in three rows: stout mechanosensory bristles and slender chemosensory hairs. The axons of all of the mechanoreceptor and chemoreceptor neurons housed in these bristles form intertwined bundles, constituting a unique nerve routed along the anterior wing margin toward the thoracic ganglion (Hartenstein and Posakony, 1989; Stocker, 1994; Couso et al., 1994). The chemosensory neurons in *Drosophila* wings are anatomically organized in spatially separated gustatory sensilla, mainly along the anterior wing margin. Their functional roles have not been documented (Hartenstein and Posakony, 1989; Stocker, 1994; Couso et al., 1994).

During flight, insect wings create air turbulence that allows sophisticated propulsion and trajectory guidance according to the physical principles of fluid dynamics (Dickinson et al., 1999; Dickinson, 2006). Amazingly, researchers have demonstrated

that the local air vortex spirals off along the wing anterior margin, where the chain of mechano- and chemosensory bristles is precisely located (Dickinson et al., 1999; Dickinson, 2006). Moreover, this neuroanatomical feature likely facilitates the subsequent capture and detection of nonvolatile tastants brought by the legs during the grooming sequences and then which are dispersed to accessible receptors by the vortex created by wing flapping. Consequently, even if gustatory receptors (GRs) are dedicated to taste perception, their putative expression in the wing is still intriguing with regard to their flight-associated functions.

The genomes of insects, such as the fly *Drosophila melanogaster*, the honeybee *Apis mellifera*, and the aphid *Acyrtosiphon pisum*, have been sequenced (Hoskins et al., 2015; Honeybee Genome Sequencing Consortium, 2006; International Aphid Genomics Consortium, 2010). Taste receptors with seven transmembrane domains have been reported for these three species using algorithms for computational searching based on structural features and on genomic databases (Clyne et al., 2000; Kim et al., 2000). In *Drosophila*, 68 GRs have been identified, and for most of them, the respective patterns of expression in taste neurons of larvae, adult legs, and proboscis are presently known (Scott et al., 2001; Robertson et al., 2003; Chyb, 2004). In aphids, 77 taste receptors have been found using sequence homology (Smadja et al., 2009). For the honeybee, only ten GRs have been described (Robertson and Wanner, 2006). Here, we report the expression of GRs identified by PCR analysis in the wing of these three species, suggesting the universality of this sensory modality.

In mammalian models, sweet-sensitive neurons transduce signals relying on receptor binding via an increase in the second messengers cyclic AMP (cAMP) and/or $\text{Ins}(1,4,5)\text{P}_3$ (Kinnamon, 2000; Lindemann, 2001; Margolskee, 2002). An increase in the cytosolic Ca^{2+} concentration occurs through both pathways, with calcium arriving either from the extracellular space through voltage-gated calcium channels controlled by cAMP levels or from intracellular stores opened by the binding of $\text{Ins}(1,4,5)\text{P}_3$ to its receptors (Lindemann, 2001; Margolskee, 2002; Amrein and Bray, 2003; Zhang et al., 2003; Medler, 2010). However, the transduction cascade of bitter molecules involves G-protein-coupled receptors, some of which activate phospholipase C, thus leading to an $\text{Ins}(1,4,5)\text{P}_3$ increase and to the subsequent opening of intracellular Ca^{2+} stores. The signaling pathways appear even more complicated because of the recent findings regarding the role of the cation channel TRPM5 in the taste

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